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THE PRIMARY COLOR-FACTORS OF LYCHNIS AND COLOR-INHIBITORS OF PAPAVER RHOEAS[1]

GEORGE HARRISON SHULL

The frequency with which the presence of hereditary characters is dominant over their absence naturally suggests that inhibiting factors may be operating when the reverse relation appears to exist, as when the hornless character of polled cattle dominates over horns, and the "smooth" character over the "bearded" in wheat, oats, etc. Some writers (DAVENPORT, BATESON, PUNNETT) have even taken the extreme view that dominance is in all cases a criterion of "presence." That this position is untenable I have shown several years ago (SHULL **11, 12**), and CASTLE (**2**) also opposes such an idea, calling attention to WOOD's well known sheep hybrids (WOOD **15**), in which the horned condition is dominant in the male and hornlessness in the female offspring from the same cross, as a proof that no such sweeping generalization is permissible. It may be granted, however, that presence is *usually* dominant, and that the dominance of the apparent absence of a character is probably in most cases, but not in all, the dominance of an inhibiting factor over its own absence. It is only necessary to keep the mental reservation that in any single instance of a putative inhibitor another hypothesis is always available, namely, that the gene for the character that is supposed to be inhibited, when existing singly as in the heterozygote, may be nearly or quite incapable of reaching the threshold of visible expression.

Both of the characters mentioned above by way of example—the polled condition in cattle and the lack of long awns in wheat—are structural characters. When a *color*-character is inhibited, the result is a "dominant white" if the inhibition of all pigmentation is practically complete, or there may result parti-colored forms exhibiting various color-patterns, or the dominance of what appears to be a lower grade of pigmentation over a higher grade when the inhibition is localized or otherwise incomplete.

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[1] Under the title "Inhibiting factors in *Lychnis* and *Papaver*," this paper was read before the Botanical Society of America, Washington, D.C., December 28, 1911. The change of title and slight changes in the text have been rendered necessary by the discovery that the purple-flowered male parent of family 10201 discussed below was probably heterozygous in both the primary factors for color. This discovery in no wise affects the general considerations presented in the paper as read, but it withdraws *Lychnis dioica* for the present as an example of dominant white.

One of the earliest known and most familiar examples of dominant white is found in the plumage of domestic fowl, in most breeds of which white is epistatic to all colors, but not always quite perfectly so. It was soon found, however, that not all of the plumages of white fowl are of the same nature, for the "Silkie" fowl's white plumage is recessive to colors. Dominant and recessive whites have been discovered in a number of other cases, both in plants and in animals. BATESON (**1**, p. 105) and GREGORY (**7**) found that white-flowered primulas with red stems are dominant whites, while those with green stems are recessive whites;[2] KEEBLE, PELLEW, and JONES (**9**), and Miss SAUNDERS (**10**) have demonstrated dominant and recessive whites in *Digitalis purpurea;* and EAST (**4**, pp. 81 f.) has shown that an inhibitor for blue aleurone-color exists in some maize plants though absent in others.

In many cases, perhaps generally, the inhibition is not quite complete, and dominant whites are often distinguishable by the possession of patches or washings of color not found in recessive whites. Similar incompleteness of action of inhibitors is seen in the occasional appearance of rudimentary horns or "scurs" in pure-bred polled cattle, in the development of a few feathers on the legs of pure clean-legged fowls, the production of short awns or "beards" on "smooth" wheat, oats, etc.

Not only are there dominant and recessive whites, but there are also different kinds of these, dependent upon the fact, now well known, that the same visible effect may be attained in various ways. It has been demonstrated that pigmentation is generally due to the interaction of at least two independent factors. When only two such factors are required, e.g., C and R, there may be three kinds of recessive whites, one lacking C, one lacking R, and

[2] While this is the general rule, KEEBLE and PELLEW (**8**) have found exceptions in the variety "Pearl," which has dominant white flowers and green stems, and in "Snow King," in which both dominant and recessive whites were found associated with dark red stems.

one lacking both *C* and *R;* and each of these whites will behave differently in certain crosses, though all are recessive to colors and may be quite indistinguishable from one another when purebred. Individuals lacking either *C* or *R*, when crossed with other individuals having the same genotypic constitution, or when crossed with individuals of the third type, which lack both *C* and *R*, will produce only white offspring; but when recessive whites of the first two types are crossed together, the complementary factors, *C* and *R*, necessary for the production of color, are brought together and a colored F_1 results, as exemplified by the classic case of "Emily Henderson" sweet peas, in which two white-flowered plants, differing externally only in the form of the pollen-grains, produced "reversionary" purple offspring when crossed together. Many similar "reversions" have been discovered by experimental breeders in a considerable number both of plants and of animals, and the old riddle of "reversion on crossing," exemplified by these phenomena, has been given a satisfactory solution in the "factor hypothesis." In so many organisms have different kinds of recessive whites been found, that their discovery in additional species no longer occasions surprise.

Less is known of the chemistry of dominant whites, but it is conceivable that these may also be of several kinds. It is plain that any pigment which is readily converted into an allied colorless compound would give a basis for a dominant white in which the pigment nucleus coexists with a factor which changes it to its colorless derivative. A suggestive illustration *in vitro* of such a reaction is the ready reduction of indigo blue ($C_{16}H_{10}N_2O_2$) in alkaline solutions to indigo white ($C_{16}H_{12}N_2O_2$). SPIEGLER (14) believed that he had succeeded in isolating a "white melanin" from white wool and white horsehair, and while GORTNER (5, 6) has been unable to confirm SPIEGLER'S conclusions in this regard, the general type of reaction suggested by SPIEGLER may be retained as possibly explaining some cases of dominant white. GORTNER (5) has proposed a very different hypothesis, namely, that as melanin is the product of an oxidase acting on a chromogen (tyrosin), dominant whites may be the result of anti-enzymes which inhibit the action of the oxidase. The same hypothesis is applicable to the widely distributed plant-pigment anthocyanin, whose method of origin appears to be in essential agreement with that of melanin. More recently GORTNER (**6**) has shown that anti-enzymes are not necessary for the inhibition in question, as the oxidizing action of tyrosinase is prevented by the presence of small quantities of such relatively simple *m*-dihydroxyl phenolic compounds as orcin, resorcin, and phloroglucin. GORTNER shows that on the basis of his investigations a satisfactory explanation can be given of those rare cases in which a white is dominant in some crosses and recessive in others, as apparently exemplified by the Shirley poppies described below.

I have been making numerous crosses among strains of *Lychnis dioica* L., and during the past six years have grown about 660 pedigreed families of this species. Nearly 300 of these families have resulted from matings between white-flowered individuals, many of the matings having been arranged for the specific purpose of finding different kinds of whites possessing complementary color-factors. Until the past summer (1911) all of these crosses between white-flowered parents have given uniformly white-flowered progenies,[3] and a similar number of crosses between white and colored individuals have invariably shown the whites to be recessive to colors, though they differed genotypically in that some of the whites carried a factor for reddish-purple and others a factor for bluish-purple, the red being epistatic to blue.

With the bringing in of two new strains of *Lychnis dioica* from their native habitats in Germany (for seeds of which I am indebted to Dr. BAUR), I have realized the complementary factors for color for which I had been looking thus far in vain.[4]

[3] The several purple-flowered individuals from white-flowered parents, mentioned in an earlier paper (SHULL **13**), appear now to have been plus-fluctuants of a "tinged white" which had not been recognized as such at the time that paper was written. They have no bearing on the problem of complementary color-factors here under consideration.

[4] That the several kinds of recessive whites exist among my Cold Spring Harbor strains, though I have not yet made a mating among them between two whites which resulted in a purple-flowered F_1, is sufficiently demonstrated by the facts presented in my earlier paper. My failure thus far to secure a purple-flowered F_1 from two whites among these strains must be due to the mere chance that I have not selected whites from the proper families.

These two forms of *Lychnis* from Germany are with apparent good reason classified by German taxonomists as distinct species, the white-flowered form being called *Melandrium album* Garcke, and the purple-flowered form *M. rubrum* Garcke. *Melandrium album*, as it appears in my cultures, has relatively narrow, spatulate, moderately ascending rosette-leaves of a rather dull dark green; the corollas are white, slender, and long-exserted from the calyx-tube; the styles are long and slender, with inconspicuous stigmatic papillae. The plants are easily grown as annuals by early sowing. *Melandrium rubrum* Garcke, grown under the same conditions, has the rosette-leaves broader, with more rounded apices; the leaves are nearly horizontal, a little darker green, and more shining. The corollas are reddish-purple, shorter, scarcely extending beyond the mouth of the calyx; the styles shorter and relatively heavy, with prominent stigmatic papillae. A very small percentage of the plants are forced to bloom as annuals, even when seeds are sown early in February. In so far as visible characters are concerned, these two forms have shown but slight fluctuations, except that in *M. album* the calyx varies from plain green through green striped with purple to a rather deep dull crimson. They have kept quite distinct from each other in regard to the characteristics enumerated, but because they breed together with undiminished fertility and because I have many other strains showing similar differences and various degrees of intermediacy, I must continue for the sake of convenience the use of the Linnean name (*Lychnis dioica*) for the entire aggregation. To what extent the other forms in my cultures may have been derived from hybridizations between *M. album* and *M. rubrum* cannot be surmised, but all strains which I have thus far found in America have presented one or more characteristics which are not directly traceable to either of the German forms, nor obviously derivable from them by recombinations of their characters. For instance, my original material of this species, collected at Cold Spring Harbor, has considerably lighter green foliage than either *M. album* or *M. rubrum*, and from the vicinity of Harrisburg, Pa., I have secured a "chlorina" (CORRENS **3**) variety having light yellow-green foliage.

Three crosses were made in 1910 between the German *Melan-*

drium album and my original white-flowered strain from Cold Spring Harbor. Two of these families (10200 and 10202) were the result of crossing two different German white-flowered females with pollen from a single Cold Spring Harbor white-flowered male. Both of these matings produced only white-flowered offspring, totaling 182 individuals. The young seedlings were indistinguishable from Cold Spring Harbor seedlings of the same age, but later they became darker green and were intermediate between the parents. A third family (1068) was essentially reciprocal to the two just described, being produced by crossing a female sib of the male used in 10200 and 10202 with pollen from a German white-flowered male. The 77 offspring were vegetatively indistinguishable from the reciprocal families, but the flowers were all reddish-purple. These different results in supposedly reciprocal crosses probably indicate that there was an unsuspected heterogeneity in the German strain. That the difference was due to heterogeneity in the Cold Spring Harbor parental family is rendered improbable by the fact that a mating (1060) between the female used as the mother of 1068 and the male used as the father of 10200 and 10202 resulted in a progeny of 73 white-flowered plants. It is unfortunate that a similar check was not applied to the German plants entering into these families, by also crossing them together. The only cross (10203) made between two specimens of *M. album* resulted in 84 offspring, all white-flowered. The mother of this family was also the mother of 10202, but the father was not the same as the father of 1068.

Several crosses were also made between the purple-flowered German *Melandrium rubrum* and my Cold Spring Harbor strains, both white-flowered and purple-flowered. Families 1092 and 1093 were produced by crossing a single white-flowered female of the Cold Spring Harbor strain with two males of *M. rubrum*, one derived from seeds collected at Furtwangen in the Schwarzwald, and the other from Oefingen in Baden. A female sib of the last-mentioned plant (i.e., from Baden) was crossed (10204) with pollen from a white-flowered sib of the mother of families 1092 and 1093. It represented a cross, therefore, as nearly reciprocal to 1093 as is possible in dioecious material. Two other families

(10206 and 10207) were produced by crossing two females grown from the Baden seeds with pollen of a single pure-bred purple-flowered male from Cold Spring Harbor. As *Melandrium rubrum* has reddish-purple flowers and as this color has been shown to be epistatic to bluish-purple (which may have been carried as a latent character by the white-flowered plants), there was no reason to expect that the F_1 progeny of any of these five crosses would present any noticeable difference in flower-color from that of their *M. rubrum* parent. This expectation was realized, the 262 offspring from these crosses all having reddish-purple flowers. The young plants in these families were generally indistinguishable from pure-bred *M. rubrum*, but later they differed by being notably more vigorous, having enormous rosettes of broad, shining, dark-green leaves. They were also much more easily grown as annuals by early sowing, being in this regard intermediate between the parents. Almost all of the hybrids were blooming by the middle of July, before the first flowers of any pure *M. rubrum* had opened.

Compared with these crosses between *Melandrium rubrum* and the Cold Spring Harbor plants, a cross of *M. rubrum* with *M. album* gave a totally different and unexpected result. A mating between a female of the white-flowered *album* and a purple-flowered male *rubrum* produced an F_1 (10201) consisting of 23 white-flowered individuals and 3 (probably 4) purple-flowered ones. The white-flowered plants were unlike either parent in vegetative characters, having relatively short, sharp-pointed, grayish-green leaves which were strongly ascending in the fully developed rosette, while both parents have long, spreading, dark-green leaves. The flowers were not only white like those of their white-flowered mother, but they were also nearly identical with them in form. It was noted that rarely some of the flowers became faintly and unevenly streaked and washed with purple just as they were fading, a feature never observed in the flowers of any of my other white-flowered plants. These white-flowered hybrids were a little later in blooming than their white-flowered parent, but were still easily induced by early sowing to behave as annuals. The purple-flowered offspring of this cross were of an altogether different character, and were not readily distinguishable in rosette and floral characters from their purple-flowered male parent. They were also like pure *M. rubrum* in not blooming until late in the season. One plant having a rosette identical with those of the three purple-flowered specimens remained a rosette, but will doubtless have purple flowers if it survives the winter.[5]

Why there should be this segregation of types in the F_1, and why one of these types should so completely resemble the male parent, while the other type was goneoclinic to the female parent, though abundantly distinct from it in the rosettes, are mysteries. Perhaps this unexpected segregation of characters in a putative F_1 is further evidence of the heterogeneity of the *M. album* material. If the white-flowered mother were heterozygous in a dominant white factor, the expected result of a cross with *M. rubrum* would be 3 white-flowered to 1 purple-flowered, or in this particular family 20 white-flowered to 7 purple-flowered, to which expectation the observed result is in sufficiently close agreement considering the small number of individuals. The same result would be attained if the *rubrum* parent were heterozygous in respect to both the primary factors for color, *C* and *R*, it being assumed that the *album* parent lacked both these factors. No other evidence of heterogeneity in *M. rubrum* has yet appeared in my cultures. It should be remarked that neither of these German strains had been pedigreed in controlled cultures, but were simply collected in separate regions in nature, so that questions as to their genotypic purity are legitimate.

In the derivatives of the corn-poppy (*Papaver Rhoeas* L.), among which are the dainty and beautiful "Shirley" poppies of our gardens, color-inhibitors are also found. According to his own statement, Rev. W. Wilks was first induced to pursue the course of selection, which resulted in the strain known as the "Shirley poppies," by discovering a bud-variation on a wild corn-poppy growing in a corner of his garden. Several flowers on this plant differed from the rest in having petals with a narrow white margin. Such a white margin is now a frequent feature of garden poppies, and when appropriate crosses are made, it is found that the presence of a margin is dominant over its absence. It is probable, therefore, that the white margin is due to the presence of an inhibitor whose action is localized in the margins of the petals.

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[5] Note added June 5, 1912. This plant is now blooming and has purple flowers as predicted.

In 1911, among 73 pedigreed families of *Papaver Rhoeas* grown at the Station for Experimental Evolution, 45 resulted from crosses between plants of which the presence or absence of a margin had been recorded, and of which a goodly proportion of the offspring were capable of being similarly recorded. The rest either had one white-flowered parent whose possession (or lack) of a margin could not be determined by inspection, or for some other reason one or both parents or the offspring could not be safely characterized with respect to margins. Of the 45 families having the margins of parents and offspring recorded, 3 represented crosses between plants both of which had margined petals, 17 were from crosses between one margined and one unmargined parent, and 25 resulted from matings between plants none of which had margined petals. The three families from matings between margined parents consisted of 236 individuals, including in each family a mixture of plants with margined and with unmargined petals. Records of the margins were often impossible, owing to the interference of other factors not yet fully investigated, so that the numbers of each type of offspring have no special significance in the present connection and they will be reserved for discussion at another time.

Of the 17 families produced by mating plants with margined and with unmargined petals, 12 were composed of a mixture of plants, some with margins and some without, 3 contained only plants with unmargined petals, and in 2 families practically all of the individuals had margins. With margins dominant over their absence, only two kinds of families were to be expected from this type of mating, namely, all margined if the margined parent chanced to be homozygous, and mixtures of plants with margined and unmargined petals if the margined parent was heterozygous. The three families (10272, 10273, 10274) in which no margins appeared, though one of the parents had a margin, are exceptions. One margined individual was the mother of all three of these exceptional families. The records show that this plant differed from the usual type, the margin being in this case red-violet[6] instead of nearly white. Whether this red-violet margin was a purely somatic modification of the dark-red body-color, or whether it was germinal, it was clearly of a different nature from the white margins involved in the other families.

In the two families (10287, 10289) whose margined parents were evidently homozygous, a small number of plants were recorded without margins. These exceptional plants occurred among those set into the garden, while larger numbers of plants from the same families, which were grown to maturity in pots in the propagating-house, were all margined. In family 10287 there were 6 plants with unmargined petals among 40 grown to maturity in the garden, and none among 133 which flowered in pots, and in family 10289 one was noted as unmargined among 47 plants in the garden and none among 83 which developed in pots. However these seven unmargined specimens are to be accounted for, it is clear that each of these families is the offspring of a homozygous margined parent.

In the 25 matings between plants, neither of which possessed margined petals, there appeared only 15 plants with margins among a total of 1402 offspring, and in a number of those recorded as margined the margin was merely a trace of lighter color of more or less doubtful character. Only in one family (10291) were the margins unmistakable, and in this family the margined plants occurred only among those which were retained in the greenhouse. Of 21 which matured in the garden none had margins, while among 99 which flowered in pots in the greenhouse there were 10 with margins, several having only a trace, while others had well marked white margins 2 mm. wide—in one plant 3 mm. wide. No attempt need be made at present to account for these few margined plants, for their number is too small to vitiate the conclusion that the unmargined condition is recessive, and that typically all the offspring of two unmargined parents are unmargined.

The most interesting matings in which margins were involved were those in which the wild poppy was crossed with its garden derivatives, for as already noted the margin is a new character which does not normally occur in the wild poppy. In the two families representing such matings, the wild poppy was used as the mother in 10298 and as the father in 10310. Both families consisted of mixtures of margined and unmargined plants, showing conclusively here also that margined petals is a dominant character, since the wild plants are certainly homozygous in the lack of such margins. The dominance of the margined condition of the garden poppies over the unmargined condition of their wild prototype is in marked contrast to all the other color-characters of *Papaver Rhoeas* yet investigated, for the dark red-orange body-color[7] of the wild poppy is epistatic to all the body-colors presented by the numerous garden forms. If dominance were a secure criterion of the presence of a gene which is absent in the recessive type, these results would indicate that while the various body-colors of the garden forms originated as retrogressive mutations, i.e., by losses of characters, the white margins of the petals represent a progressive mutation through the addition of a gene which inhibits the development of color in that region. Doubleness also proves to be dominant over the single type of the wild poppy, and, on the basis of the same assumption, would have to be classed as a progressive mutation. I cannot forbear, however, to repeat the caution that dominance does not necessarily demonstrate the progressiveness of a mutation, since the alternative hypothesis, mentioned above in the first paragraph, allows for the dominance of a character which has originated by a retrogressive mutation.

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[6] The color-nomenclature adopted in this paper is based on the spectrum colors, as arranged in the Milton Bradley system. Exact shades and tints have been recorded, but for the sake of simplicity these have not been reproduced here.

There is still one other color-inhibitor (possibly several) in the derivatives of *Papaver Rhoeas*, which is in some respects more noteworthy than that which produces the white margins. This affects the body-color of the petals, producing what is essentially a dominant white, though in this case the inhibition is not usually complete and the flowers often show some irregular striation of dull violet, reddish, or bluish color on the petals, especially in the presence of purple stamens.

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[7] By the expression "body-color" it is intended to indicate the color of the general intermediate region of the petals as distinct from "center" (proximal) and "margin" (distal).

A single white-flowered plant with yellow stamens was crossed in 1909 with three red-flowered plants (yielding families 10275, 10281, 10282) and with two plants having dull striations on the petals (families 10280, 10283), and the offspring of these five matings were generally white or whitish-flowered. Of 559 plants in these families only 25 were neither pure white nor white with traces of reddish color, and of these 25, all that had a full red (i.e., not striated) parent were lighter in color than that parent. These fully pigmented offspring may simply represent minus-fluctuations in the action of the inhibitor derived from the white-flowered parent. If this is the correct interpretation of these few plants with colored flowers, it should be possible to secure from them progenies displaying the presence of the inhibitor though it be invisible in both parents. While I have as yet grown no offspring from the colored plants of these families, I have two other families (10270, 10308) in which the same whitish offspring have appeared, though both parents in each case were fully pigmented. Family 10270 was produced by mating two dark-red parents which were sibs in a family consisting of red, red-orange, pink (light violet-red), and white. The progeny of these two dark-red plants consisted of 68 white or whitish and 70 pigmented, the latter often striated and generally much less intensely pigmented than either parent. Only two of the offspring showed as deep shade as that of their parents. The parents of family 10308 were also red-flowered sibs in a family containing red, red-orange, pink, and white. They were considerably lighter red than the parents of 10270, but were fully and evenly pigmented. Their offspring consisted of 80 white- and whitish-flowered plants and 13 with pigmented flowers, none of which were as deeply pigmented as either parent, and several of which showed the peculiar striation which seems to be one of the manifestations of the inhibitor believed to be operating in these crosses. Similar results were obtained in seven families (10266, 10273, 10274, 10297, 10303, 10305, 10311) produced from mating together two plants with striated petals, or a striated with a plain red, and only in one family, containing three individuals (10268), did the "dominant white" fail to manifest itself in progenies from matings of this character. In the latter family a cross between a light-red and a striated individual produced three offspring, all with flowers slightly darker red than those of their red-flowered parent. Considering the complexity of some of these families, this number of individuals is entirely inadequate for the deduction that family 10268 was really exceptional.

While I have laid no emphasis thus far on the fact, it may have been noted that all of these poppy-families in which a "dominant white" has made its appearance have been derived from red or striated parents, never from red-orange or pink (light violet-red). It seems that the factor under discussion is not a general inhibitor of color but only of pure spectrum-red. The following facts seem to prove this: The same white-flowered plant with yellow stamens which we have seen producing white-flowered progenies when mated with red (families 10275 and 10281) was also mated with two homozygous pink-flowered plants (families 10277 and 10278) and a homozygous red-orange plant (10279) and in all of these three crosses the white-flowered parent proved to be a recessive white. Families 10277 and 10278 consisted of 43 pink-flowered and 25 red-flowered plants, and 10279 contained 226 red-orange-flowered plants and 1 red-flowered. Not a single individual in any of these three families had white or whitish flowers. In keeping with these results are families in which striated plants were mated with pink (10295) and red-orange (10301), for in neither of these families appeared a white-flowered offspring or one with striations, 10295 yielding 37 pink-flowered and 33 red-flowered and 10301 giving 22 which were red-orange and 5 intermediate between this and red.

The occurrence of many red-flowered plants in these families, when one of the parents supposedly contained an inhibitor for red, is not satisfactorily explainable on the assumption made above, that there is a single inhibitor for red whose effectiveness fluctuates to such an extent that its presence may not be detected in its extreme minus-fluctuations. An alternative hypothesis may be suggested, which must await further experimentation for its confirmation or rejection. If there be two factors, A and B, which are ineffective when existing apart from each other, but which become an inhibitor when acting together, the observed results could be explained by assuming that in those matings which produced whitish-flowered offspring, the one parent possessed *A*, the other *B*, while in those matings in which a fully pigmented progeny was produced, the two parents had the same factor—either both *A* or both *B*—or else one of them lacked both *A* and *B* and the other parent lacked one of them. The occurrence of fully pigmented individuals in association with "dominant whites" need not then be minus-fluctuations of a single inhibitor, but might be the result of segregation of inhibiting factors, one or more of which were heterozygous in one or both parents.

Summary

Dominant and recessive whites have been discovered in a number of different plants and animals. Both the dominant whites and the recessive whites may be of different kinds, though externally indistinguishable.

Dominance does not necessarily indicate presence of an added gene, but when the absence of a character appears to be dominant over its presence, the action of an inhibiting factor may usually be inferred. An alternative hypothesis is always available, however, which should prevent a too dogmatic assertion that dominance is synonymous with presence.

A white-flowered form (*Melandrium album*) of *Lychnis dioica* L. from Germany, when crossed with the purple-flowered form (*M. rubrum*) from the same country, produced 23 white-flowered and 4 purple-flowered offspring, but in certain crosses with a white-flowered strain derived from plants growing at Cold Spring Harbor, the German white-flowered plants produced purple-flowered offspring in the F_1, in other crosses only white-flowered offspring were produced.

In the "Shirley" poppies (*Papaver Rhoeas* L.), the presence of a white margin of the petals is a dominant character and is probably due to an inhibitor limited in its effective action to the margins of the petals.

These white margins and doubleness of the flowers are the only characters in the garden poppies which were found dominant over the corresponding characters of the wild type from which they

were derived. They may represent the results of progressive mutations, but here again caution is necessary because of the alternative hypothesis.

There is also an inhibitor which affects the body of the petals in the "Shirley" poppies, producing what is essentially a dominant white, though the inhibition is often very imperfect, in which case the flowers are more or less washed and striated with color, though generally whitish.

This supposed inhibitor was evident only in crosses involving at least one red-flowered or striated parent. The same white-flowered plant which was a dominant white in crosses with red-flowered and striated plants was a recessive white in crosses with pink-flowered and red-orange-flowered plants.

In several cases red-flowered plants crossed together produced a whitish progeny and a similar result was produced when two striated plants were mated or when striated was crossed with red.

Two hypotheses to account for these facts are considered: (*a*) that there is one inhibitor affecting only the pure spectrum-red and having no effect on pink and red-orange; the minus-fluctuations of this inhibitor pass the limit of visibility; (*b*) that there are two factors, *A* and *B*, which have no visible effect when existing alone, but which act as an inhibitor when brought together. These two hypotheses must be tested by further breeding.

I take pleasure in acknowledging here the faithful work of Mr. E. E. BARKER, who assisted me in making the records upon which this paper is based.

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